

THE ZOOLOGICAL REGION OF SOUTHERN AFRICA AS DEDUCED FROM THE COMPOSITION OF ITS LACERTILIA.

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FOR purposes of convenience, zoological systematists have defined the northern boundary of the South African sub-continent in a variety of ways, and the dividing line now most generally accepted—from the Zambesi on the east to the Cunene River on the west—has no claim to be considered as a rigid natural boundary, for there is an extensive overlapping of the South African and tropical faunas.

At the same time, as I hope to show in this paper, there certainly is in the southern portion of Africa a fauna sufficiently peculiar to justify our regarding this region as a definite zoological area; and, for example, its fauna is much more distinct from that of the rest of Africa than is the Bornean fauna from that of the Malay Peninsula, though in this case the land areas are separated by several hundred miles of sea. Further, the distribution records show that the area in question resolves itself into several zoological sub-regions, a fact which was pointed out by Professor Max Weber (*Zool. Jahrb.*, bd. 10, 136) from consideration of the fresh-water fish fauna.

During the earlier part of this paper the term South Africa will be employed in its orthodox sense, i.e. Africa south of the Zambesi and Cunene Rivers, but later on I shall bring forward evidence to show that a more natural region is Africa south of the equator, the Congo basin excluded; the term tropical as applied to a genus or species will here imply nothing more than that it occurs in Equatorial Africa, or north of the equator, but is not endemic in South Africa, though it may occur here.

The dual nature of our reptilian fauna, consequent on the overlapping of the tropical species, is very obvious in the northern portions of the sub-continent, and is not prominent in south-west Cape Colony; indeed, in passing southwards from the Zambesi to Cape Colony, there is a gradual and successive disappearance of the widely-distributed tropical forms simultaneous with the appearance of an increasingly greater proportion of peculiarly South African species. As an introduction to this subject, it will be profitable to consider the fauna of this immediate neighbourhood, and the following is a list of the reptilia and amphibia of Pretoria, an asterisk denoting forms which occur also in tropical Africa—

Lizards.

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| <i>Pachydactylus capensis</i> Smith. | <i>Eremias lineocellata</i> D. B. |
| * <i>Lygodactylus capensis</i> Smith. | <i>Ichnotropis capensis</i> Smith (occur-
ring also in Angola). |
| <i>Agama hispida</i> var. <i>distanti</i> Boul. | * <i>Gerrhosaurus flavigularis</i> Wieg. |
| * <i>Agama atricollis</i> Smith. | <i>Mabuia trivittata</i> Cuv. |
| <i>Zonurus jonesii</i> Boul. (also in
Angola). | * <i>Mabuia striata</i> Pet. |
| <i>Zonurus vittifer</i> Reich. | * <i>Mabuia varia</i> Pet. |
| <i>Chamaesaura aenea</i> Fitz. | * <i>Lygosoma sundervalli</i> Smith. |
| * <i>Varanus niloticus</i> Linn. | * <i>Ablepharus wahlbergii</i> Smith. |
| * <i>Nucras tessellata</i> Smith. | * <i>Chamaeleon quilensis</i> Boc. |

Snakes.

- Glauconia distanti* Boul.
Typhlops bibroni Smith.
Ablabophis rufulus Licht.
* *Boodon lineatus* D. B.
Pseudaspis cana Linn.
* *Leptodira hotamboeia* Laur.
* *Lycophidium capense* Smith.
Chlorophis natalensis Smith.
* *Chlorophis hoplogaster* Günth.
* *Naia haie* Linn.
Sepedon haemachates Lacép.
Homorelaps dorsalis Smith.
* *Homalosoma lutrix* Linn.
- * *Dispholidus typus* Smith.
* *Psammophis sibilans* Linn.
Psammophis furcatus Pet.
* *Trimerorhinus tritaeniatus* Günth.
Trimerorhinus rhombeatus Linn.
(also in Angola).
* *Tarbophis semiannulatus* Smith.
* *Dasypeltis scabra* Linn.
Causus rhombeatus Licht.
Atractaspis bibroni Smith. (also
in Angola).
* *Bitis arietans* Merr.
* *Python sebae* Gmel.

Frogs.

- * *Rana angolensis* Boc.
Rana fasciata Tschudi.
Rana natalensis Smith.
* *Rana adspersa* Tschudi.
* *Rana delalandi* Tschudi.
- * *Phrynobatrachus natalensis* Smith.
* *Cassina senegalensis* D. B.
* *Bufo regularis* Reuss.
* *Bufo carens* Smith.
* *Xenopus laevis* Daud.

A number of these asterisked species belong to the tropical fauna, but some are really South African species which have extended northwards. The preponderance of tropical forms in any single locality is considerably greater than is the case when a large area is comprised, for whilst the tropical fauna in South Africa is on the whole a heterogeneous assembly of unrelated species which are widely distributed over large areas, the endemic fauna is composed of sets of closely related species which are more strictly localized in distribution, and the areas occupied by such species do not much overlap.

Unfortunately, it is not possible for me to give a list of the Capetown fauna for comparison with the preceding, and for the present it must suffice to say that the majority of the tropical species have their southern limit in some part of Eastern Cape Colony, whilst only a very small percentage reaches as far as Capetown.

The following statistics relate to this question of overlapping of faunas:—South Africa has about 136 species of lacertilia, of which forty-four are found beyond the northern boundary; in Angola, Bocage recorded sixty-two species of lacertilia, of which thirty-one occur also in South Africa; in German East Africa, Tornier (*Zool. Jahrb.*, 1900, p. 579) records sixty-five species of lacertilia, twenty-three of which also occur in South Africa; Mr. Boulenger's list of the Whyte Collection from North Nyassaland (*P. Z. S.* 1897, p. 800) comprises fourteen species of lacertilia, of which eleven occur also in South Africa; in Somaliland [Boulenger, *Annal. Mus. Civico. storia. Nat. Genova Serie 2a*, vol. XVII (XXXVII)], seventy species of lacertilia are recorded, of which ten occur also in South Africa; in Egypt, the only lizards also to be found in South Africa are four species, as follows:—*Varanus niloticus*, *Mabuia quinquetaeniata*, *Gerrhosaurus flavigularis*, and *Agama colonorum*, which last-mentioned doubtfully occurs in South Africa.

We may now turn to a general consideration of the lizard fauna of South Africa, from point of view of the distribution of the species and their relationships. The lacertilia of South Africa are composed as

follows :—Geckonidae twenty-seven species, Agamidae about ten species, Lacertidae twenty species, Zonuridae sixteen species, Gerrhosauridae ten or eleven species, Scincidae thirty species, Varanidae two species, and Chamaeleontidae ten species.

Geckonidae.

Eleven genera are known, of which a good proportion are characteristically South African. *Palmatogeco*, *Chondrodactylus* and *Colopus* are, so far as is known, confined to South Africa; they are restricted to the western portion of the sub-continent and are probably all monotypic genera.

The genus *Homopholis* has one (or two) species in the eastern portion of South Africa, a species is recorded from Abyssinia, and another species occurs in Madagascar. The genus *Oedura*, which is otherwise known only from Australia, has two representatives in South Africa, and the genus does not occur in any other part of Africa.

The genus *Pachydactylus*, comprising thirteen or fourteen species, all confined to Africa south of the Equator, has twelve species in the South African region. *P. bibroni* has a very wide distribution ranging northwards into Tropical Africa, but it should be regarded as truly South African, as it belongs to a section of seven recorded species of which all the other members are confined to South Africa. *P. ocellatus* is common in western Cape Colony, and is also recorded from Benguela and from Ascension Island. This genus reaches its greatest development in Cape Colony and the western portion of the sub-continent; only one species, *P. punctatus*, is confined to the eastern portion (Mozambique, Zoutpansberg District) of our region.

Rhoptropus, a genus of three (or two) species, is only known from the western portion of southern Africa. *R. ocellatus* occurs in western Cape Colony, and *R. afer* is known from German South-West Africa and Angola. According to Dr. Jean Roux, however, this genus is identical with *Phelsuma*, a genus of eight or nine species occurring in East Africa, Madagascar, Comoro, Zanzibar, Mauritius, Bourbon, Rodriguez, Seychelles, and Andaman Islands. The genus *Elasmodactylus* has one species in British Namaqualand (*vide* Sclater) and another in the lower Congo region. *Lygodactylus*, a genus occurring in tropical and South Africa, and in Madagascar, has two representatives in South Africa. One of them, *L. capensis*, closely related to a Madagascar species, occurs in the tropics and extends southwards into eastern Cape Colony; the other species, *L. ocellatus* Roux, is only known from the Transvaal. *Ptenopus garrulus* Smith, the only species of the genus, is known from German South-West Africa and north-west Cape Colony.

Phyllodactylus, a large genus recorded from the tropics of America, Australia, and Africa, has two species in South Africa, of which the better known *P. porphyreus*, occurs also in the Congo region, Madagascar, and Australia (assuming the identity of this species with *P. marmoratus* of Australia); the only locality known to me for *P. lineatus* is Laingsburg, C.C. (Roux).

Hemidactylus is almost a world-wide genus within the tropics. Only one species occurs within our area, and this *H. mabouia* is common to tropical Africa, Madagascar, West Indies, and South America. It is evident that the gecko fauna of South Africa is very characteristic and with a good proportion of endemic genera is well marked off from the tropical gecko fauna (which is comparatively poor in number of species

and has no peculiar genera), though one or two representatives of the latter extend southward into the sub-continent. The affinities of these endemic genera are as follows : the isolated genus *Chondrodactylus* is closely allied to the *Nephrurus* of Australia ; *Phyllodactylus* is very near the Madagascar genus *Ebenavia*, and in the same group with these is *Oedura*, which is Australian and South African, and two other genera belonging to Australia and Southern India respectively.

The genera *Pachydactylus*, *Colopus*, *Rhoptropus*, *Elasmodactylus*, and *Phelsuma* (which, perhaps, includes *Rhoptropus*), constitute a distinct group of genera, the three former being South African, the fourth belonging to Lower Congo and British Namaqualand, whilst *Phelsuma* belongs to East Africa, Madagascar, and other islands of the Indian Ocean. *Homopholis*, belonging to South Africa, Abyssinia, and Madagascar, has generic relationships in Madagascar.

The genus *Lygodactylus*, which has several species in tropical West Africa and in Madagascar, but only one species peculiar to South Africa, has its nearest ally in another Madagascar genus ; apparently the West African forms constitute a section of the genus distinct from that which includes the South African and Madagascar species. The genus *Ptenopus* has its nearest relative in *Stenodactylus*, a genus belonging to North Africa and South-West Asia. The isolated *Palmatogecko* is considered by the describer of this genus to be related to *Ptenopus*.

It should be mentioned that the affinities above cited are taken from the classification employed by Mr. Boulenger in the B. M. catalogue, and this is based upon characters which are largely adaptative. I believe, however, that these relationships are for the most part quite true, for otherwise we should have to suppose that a process of convergent evolution has taken place in the case of a number of pairs of genera belonging to South Africa and Madagascar. And, again, it is a well known fact that geckos are particularly well adapted for accidental transportation over great distances, as they occur on many oceanic islands, so that this might be a partial explanation of the occurrence of South African genera and allies in Madagascar ; but this supposition loses value when we remember that many of the geckoes of South Africa are rather localized in distribution, and that, whilst South Africa and Madagascar have each a rich gecko fauna, only very few representatives of these faunas are found north of the equator.

Agamidae.

This family is represented in South Africa by about nine or ten species of the genus *Agama*. There are only three genera in the whole African region, and Madagascar has no representatives whatever of this family.

The South African species, *A. hispida*, its variety *distanti*, *brachyura*, *aculeata*, *armata*, *pulchella*, *atra* and *holubi*, constitute a structurally distinct association, the members of which are confined to South Africa, with the exception of *armata*, which extends up into Angola and German East Africa, and *hispida*, which is also known from German East Africa.

A. kirki, *mossambica*, and *planiceps* found in the northern portions of the sub-continent and in tropical Africa belong to an association of tropical and North African species.

A. atricollis, which occurs in German East Africa and Angola, extending southwards as far as Natal, has a near ally in Abyssinia and Arabia, and belongs to a section of species which are mostly found in Persia and North India.

In brief, the Agamoid fauna of South Africa has no peculiar genera and is not very distinctive; it comprises six or seven endemic species and several species which belong to the overlapping tropical area.

The genus *Agama* is principally African, and has representatives also in south Asia and south-east Europe.

Zonuridae.

This whole family is characteristically South African, being confined to Africa south of the equator, with an odd species in Madagascar. Mocquard doubts the latter record on the grounds that the only evidence is in Cope's original description, which is not authenticated with the usual data, whereas it is now known that the species occurs in German East Africa; at the same time the fact that the species of *Zonurus* are often exceedingly localized in their distribution may explain the former part of the argument whilst it does not preclude the possibility of a disconnected distribution at the present day. There are four genera, the largest, *Zonurus*, comprising about ten species, of which eight occur in South Africa and only two of these (*Z. cordylus* and *jonesii*) extend northward into the tropical region (fide Tornier and Bocage). The species of *Zonurus* distribute themselves all over the South African region, some of the species being probably very localized (cp. *capensis*, *warreni*, and *giganteus*). The monotypic genus *Pseudocordylus* occurs along the coastal strip of Cape Colony and extends northwards in the eastern portion of the sub-continent as far as the Zoutpansberg District.

The genus *Chamaesaura* has three species in the eastern portion of the sub-continent: one of these *C. macrolepis* is also recorded from Angola. The tropical species of this genus occur in Uganda, British Central Africa, and German East Africa.

The genus *Platysaurus* has four species of which three are distributed in South Africa, one western and two eastern, and the fourth species *P. torquatus* occurs in Mozambique (precise locality unknown).

From these facts of distribution it would seem highly probable that the family has been evolved in Southern Africa.

Varanidae.

Only two species occur in South Africa of which one, *Varanus niloticus* is common to almost the whole of Africa whilst the other *A. albigularis* occurs also in South Angola and in Nyassaland. The genus occurs in Africa, India, Malay Archipelago, and Australia, but not in Madagascar.

Amphisbaenidae.

Three genera are known in South Africa, but they form no characteristically South African association of species.

The genus *Amphisbaena* represented by a number of species in the tropical portions of America and Africa has two species in South Africa: *A. violacea* extends from Zululand to Mozambique and *A. quadrifrons* occurs in Hereroland and as far south as Kimberley.

The genus *Monopeltis* has about four species in South Africa of which probably all extend north of the boundary line: *M. capensis* and *anchietae* are western species whilst *sphenorhynchus* and *granti* (this latter only known from Beira) are eastern. This is an African genus of about a dozen species; its headquarters are West Africa.

Chirindia is a monotypic genus known only from south-east Mashonaland. So far as I know Amphisbænidae are not recorded from Cape Colony and the South African representatives are best regarded as outlying members of a tropical group.

Lacertidae.

Five genera occur in South Africa, and one of them, the monotypic *Tropidosaura*, is peculiar to the region being known only from the coastal strip of south Cape Colony. The genus *Eremias* has nine species in South Africa, of which seven are western forms (*capensis*, *undata*, *lugubris*, *suborbitalis*, *namaquensis*, *pulchella* and *inornata*), all of them being found in Namaqualand, and several extending into the Karroo region of Cape Colony, whilst *lugubris* and *namaquensis* also occur in Angola. *E. burchelli* appears to be confined to Cape Colony and *lineocellata* occurs in the Transvaal and Orange River Colony. The genus is not known to occur in Natal and Zululand.

Eremias is a large genus, well developed in Africa, and occurring also in Asia. The South African species, for the most part, do not form a structurally distinct association, but their relationships are with the other African species; a small more or less distinct natural group is constituted by the four species: *pulchella*, *lineocellata*, *burchelli* and *capensis*. The genus *Nucras* has only two species: *N. delalandii* occurs in the Eastern portion of the sub-continent, extending southward along the coastal strip of Cape Colony, and northwards perhaps as far as German East Africa, whilst *N. tessellata* is widely distributed over tropical Africa and South Africa, with the exception of southern Cape Colony.

The genus *Scapteira* has five representatives in South Africa, one in Mossamedes and three in Central Asia. The South African species are all western forms with the exception of *S. knoxii*, which belongs to Cape Colony, extending eastwards at any rate as far as Kingwilliamstown, and is recorded (B. M. Cat.) from the Island of Johanna. The species *knoxii*, *depressa*, *serripes*, and the Angola species, form a distinct natural group, and the two remaining South African species, *ctenodactyla* and *cuneirostris*, constitute another distinct group. The disconnected distribution of the genus *Scapteira* is somewhat remarkable in view of the fact that both the Asiatic and the South African habitats are deserticolous, and that like conditions prevail in a great part of the intervening area; and the presence of *S. knoxii* in Johanna Island seems to be inexplicable, especially as Madagascar has no *Lacertidae*.

The genus *Ichnotropis* is confined to Africa south of the equator. *I. squamulosá* is a tropical species extending southwards about as far as the northern border of Cape Colony, whilst *I. capensis* occupies a wide strip of country from Natal in the east to Angola in the west; *longipes*, which is very closely allied to *capensis*, is described from Mashonaland.

The lacertid fauna of the sub-continent as a whole is not very distinct, though there is one peculiar genus, the monotypic *Tropidosaura*, which is closely related to the other African genera; the South African representatives are, indeed, a part of the general Ethiopian lacertid fauna, and this family furnishes very little positive evidence in favour of the maintenance of the South African area as an absolutely distinct zoological region.

Gerrhosauridae.

This family has its headquarters in South Africa and Madagascar. Of the five genera, three occur in our area and two are peculiar to Madagascar. The genus *Gerrhosaurus* has about five or six species, of which one species, *typicus*, is only known from north-west Cape Colony : *flavigularis* is found almost throughout tropical (not in West Africa) and South Africa ; *validus* occupies a strip of country from South Angola to the Zoutpansberg District ; and *major* is principally an eastern species ranging from East Africa to Natal. I regard the genus *Gerrhosaurus* as truly South African, though several of the species do extend beyond the northern boundary. Amongst the lizards it is a general rule that species of undoubted tropical relationship do not extend southward into south-west Cape Colony (cp. *Mabuia striata*, *Lygosoma sundevalli*, *Ablepharus wahlbergi*). On the other hand, *Gerrhosaurus flavigularis* does occur in south-west Cape Colony, in spite of its extensive range within the tropics ; and this is the case also with *Pachydactylus bibroni* and other South African species of like distribution. Again, *Gerrhosaurus major*, until recently, was known only from Zanzibar Island, but has since been recorded from German East Africa, and from Togoland in West Africa. In 1907, Mr. Boulenger described *grandis* from Zululand, but from the evidence of material from the Barberton District I have reduced *grandis* as a synonym of *major*. *G. bergi* of German East Africa appears to be very closely allied to *major*, and so also is *G. bottegi*, described from Erithraea.

The genera *Tetradactylus* and *Cordylosaurus* are characteristically South African. The former has four species : *T. seps* occupies the coastal strip of Cape Colony, *T. tetradactylus* is only known from south-west Cape Colony, *T. breyeri* is a Natal and Transvaal species and *T. africanus* is recorded from Natal, Namaqualand, and South Angola.

Cordylosaurus trivittatus ranges from western Cape Colony as far as South Angola and *C. tessellata*, doubtfully distinct, is recorded from Namaqualand.

Scincidae.

Nine genera of Scincidae occur in South Africa. The large genus *Mabuia* which though principally African occurs all over the warmer parts of the world except Australia, has twelve species in South Africa but these do not constitute a peculiar group or groups : *striata*, *varia*, and *quinquataeniata* are tropical forms which descend southwards as far as eastern Cape Colony : *stangeri*, *occidentalis*, *acutilabris*, *sulcata*, and *peringueyi* are western species, none of them extending as far south as the southern coastal districts of the Cape Colony and all excepting the last mentioned occurring in South Angola : *trivittata*, apparently occurs throughout South Africa with the exception of Natal, Zululand, and Rhodesia, and this species belongs to a small section which includes also *occidentalis* and *ivensii* which are both western species : *homalocephala* occupies the coastal strip of South Africa, *depressa* (possibly a synonym of *homalocephala*) is only known from Tette, and *gruetzneri* from Gerlachs-hoop (Transvaal).

The very large genus *Lygosoma*, mainly Australian but almost cosmopolitan in the tropics except for Madagascar, has only five or six species in tropical Africa and but one, *sundevalli*, extends southwards into the subtropical parts of South Africa,

Ablepharus wahlbergi, the only representative in South Africa of a widely-distributed old world genus, has a very similar distribution : of this genus, four species occur in tropical Africa and one species which is nearly cosmopolitan occurs in Madagascar.

The genus *Acontias* has about eight or nine species, and is known from South Africa, Madagascar, and Ceylon. *A. meleagris* occurs throughout South Africa, *plumbeus* is an eastern species ranging from East Cape Colony to Mozambique, and *lineatus* is a western species extending eastwardly across the Karroo.

The genus *Scelotes* occurs in South Africa, Madagascar and Mauritius, and out of a total of twelve or thirteen species, South Africa has six. The South African and Madagascar species range themselves into distinct groups, except that one of the Madagascar species has its nearest ally in *S. capensis*. The species *capensis*, *bicolor*, *caffer*, and *tridactylus* are western or Karroo forms ; *bipes* is found in the coastal regions of Cape Colony and Natal, whilst *guentheri* and *inornatus* are eastern forms, occurring in Zululand and Natal.

Herpetosaura is a South African genus of three species ; *anguina* occurs in Kaffraria, *mira* is a Transvaal species, and *arenicola* occurs in Natal, Zululand, and Mozambique.

The genus *Sepsina* has about ten or eleven species in Madagascar, tropical and South Africa. *S. weberi* is only known from Little Namaqualand, and *grammica* is indefinitely located on the south-west coast of Africa.

The genus *Typhlacontias* has two species, one in Mossamedes and the other, *gracilis*, in the Zambesi district.

The genus *Melanoseps*, with only one species, *ater*, extends from German East Africa into Mozambique.

I believe that the Scincidae of South Africa are for the most part of single origin, though at first sight this may not seem to be the case ; the vermiform genera, *Acontias*, *Scelotes*, and *Herpetosaura*, etc., certainly constitute part of the peculiarly South African fauna, whilst the species of *Mabuia*, *Lygosoma*, and *Ablepharus* genera, which are so widely distributed, may be more recent arrivals from elsewhere. But the species of *Mabuia* at any rate should be included in the endemic fauna, seeing that the genus is principally African and is well represented in South Africa and also in Madagascar ; the distribution of the genus may possibly be explained in the same way as that of the chamaeleons (see later) or perhaps on the grounds of its antiquity.

Anelytropidae.

This small family of worm-like lizards has a genus in each of the three areas Mexico, West Africa, and South Africa, but according to Gadow this is quite an artificial assembly of degenerates and no great importance is to be attached to the facts of distribution. The South African *Typhlosaurus* has five species, of which *lineatus* and *vermis* are known from north-west Cape Colony, *cregoi* from the Zoutpansberg District, *aurantiacus* from Zululand and Mozambique, whilst the precise locality of *caecus* is unknown.

Chamaeleontidae.

Ten species of Chamaeleon and one Rhampholeon occur in South Africa,

The genus *Chamaeleon* has its headquarters in Madagascar and Africa, and there are one or two isolated species in Arabia, Ceylon, and Southern India. The species *melanocephalus*, *taeniobronchus*, *gutturialis*, *caffer*, *pumilus*, *ventralis*, and *damaranus* form a distinct and characteristic South African group: they are mostly Cape Colony forms, several extending into Natal, whilst *damaranus* ranges between Knysna (Cape Colony) and the Zoutpansberg District. Mocquard has recorded *C. melanocephalus* from Madagascar, but in his recent work on the Madagascar reptiles (Nouv. Archiv. du Museum d'Hist. Nat., Paris, 1909) this species has no place in the faunistic list.

The nearest relatives of this South African group of Chamaeleons are *C. tigris* of the Seychelles (and Zanzibar Islands?), *fuellieborni* from German East Africa, *jacksoni* from Uganda, *bitaeniatus* of East Africa, and *tempeli* of German East Africa (Werner, Zool. Jahrb. 1902, p. 295).

C. namaquensis is a western species stretching from South Angola into western Cape Colony, the most eastern record being Kimberley: this species is quite isolated in the genus. The species *dilepis* and *quilenis*, referred by Tornier to one and the same species, are tropical forms occurring in West Africa and German East Africa and extending southwards as far as the Orange River.

Rhampholeon marshalli, the only representative in South Africa of a tropical genus, comes from the Chirinda forest in south-east Mashonaland.

Having thus briefly surveyed the distribution of the various groups of South African lizards, the following facts present themselves:—

(1) One family, the Zonuridae, is almost peculiar to the region, but may have a representative in Madagascar, and another family, the Gerrhosauridae, has its headquarters in South Africa and Madagascar.

(2) In the Geckonidae and the Scincidae there are a good proportion of genera which do not occur in tropical Africa, some of them being peculiar to South Africa, whilst others are represented also in Madagascar, and several in Southern India and Australia.

(3) Several large and widely-distributed genera occurring also in tropical or northern Africa are represented in South Africa by an association of species which is structurally separated from the other sections of the same genus, but in other cases the South African representatives do not form a distinct group.

(4) In some families (Agamidae, Varanidae, Scincidae, etc.) a number of tropical species have extended southwards into South Africa.

And we may refer the lizard fauna of South Africa to three classes:—

(1) The peculiar endemic fauna, comprising the Zonuridae, Gerrhosauridae, all the Geckonidae with the exception of *Hemidactylus*, and the Scincidae, with the possible exception of *Lygosoma* and *Ablepharus*.

(2) The Chamaeleons, which are very characteristic of the whole Ethiopian region, but unlike other families which are well developed in Madagascar, they are not restricted to southern Africa, but occur throughout the whole of Africa.

(3) The "Ethiopian" fauna, including the Agamidae, Lacertidae, Varanidae, *Hemidactylus* in the Geckonidae, the *Amphisbaenidae*, and possibly the Scincoid genera, *Lygosoma*, and *Ablepharus*. This fauna is composed of genera which for the most part have a wide range through Africa and often through Southern Europe and Asia, but this whole assembly may not be of single origin.

As we have already mentioned, a number of genera comprised in the peculiar fauna have relationships in Madagascar, and indeed this fauna as a whole has a very strong affinity with the whole Madagascar fauna.

The lacertilia of Madagascar are composed of the following families : Geckoes, Skinks, Chamaeleons, Gerrhosauridae (Zonuridae probably), and a few Iguanidae, whilst the other families Agamidae, Varanidae, Lacertidae, Anguidae, and Amphisbaenidae are quite absent; leaving out of consideration the Iguanidae—the occurrence of which in Madagascar has not yet been satisfactorily explained—the Madagascar lizard fauna shows complete identity in its families and identity or close relationship in many of the genera with the peculiar fauna of South Africa, and the families which are lacking to Madagascar are those which constitute what I have termed the Ethiopian fauna of South Africa.

It should be mentioned, however, that the identity of the faunas does not extend to the species, for probably there is not a single species of lizard common to Madagascar and South Africa, and further, Madagascar has a few peculiar genera which have no allies in South Africa.

Again, this peculiar fauna is not strictly limited on the north by the Zambesi and Cunene Rivers, and as a matter of fact it is to be found to some extent right up to the equator. In Tornier's list of the lizards of German East Africa we find the following representatives of this fauna :—

Geckonidae : Pachydactylus, 2 sp. ; Platypholis, 1 sp. ; Diplodactylus, 1 sp.

Zonuridae : Zonurus, 2 sp. ; Chamaesaura, 1 sp.

Gerrhosauridae : Gerrhosaurus, 1 sp.

Scincidae : Sepsina, 1 sp. ; Melanoseps, 1 sp.

And in Angola, according to Bocage, there are :—

Geckonidae : Pachydactylus, 2 sp. ; Rhoptropus, 1 sp.

Zonuridae : Zonurus, 2 sp. ; Chamaesaura, 1 sp.

Gerrhosauridae : Gerrhosaurus, 2 sp. ; Tetradactylus, 1 sp. ; Cordylus, 1 sp.

Scincidae : Sepsina, 3 sp. ; Typhlacontias, 1 sp., but with very few exceptions—the genera *Lygodactylus*, *Homopholis*, and *Gerrhosaurus*—this fauna does not pass north of the Equator.

The dual nature of the South African fauna and the general relationship of the one portion with that of Madagascar is no doubt to be explained by the following old theory : Madagascar, according to most authorities, was united with Southern Africa up to midtertiary times (Mocquard and others consider that the separation occurred in the secondary period) this large area constituting a continental island (see "Wallace's Island Life"), and there was a common fauna which gave rise in South Africa to the peculiar endemic fauna of the present day. Then came the separation off of Madagascar, and subsequently the continent of Africa assumed its present shape and South Africa was invaded by a new assembly of lizards, Lacertidae, Agamidae, etc., which came from Europe and Asia via North Africa. It is not possible for me to deal with the problem of the primary origin of the peculiar fauna of South Africa and of Madagascar, for the affinities of such characteristic families as the Gerrhosauridae and the Zonuridae provide no very definite clue, nor is there any palaeontological evidence ; but as there seems to be no indication that this is derived from a European or Asiatic source, it may perhaps be regarded as the remains of a former southern hemisphere fauna, for it has some relationship (*Scincidae*, *Geckonidae*) with Ceylon, Southern India, and Australia (cp. distribution and relationship of

the genera *Acontias*, *Sepsina*, *Melanoseps*, *Oedura*, *Phelsuma*, and *Phyllo-dactylus*); and though the evidence of these few lizards is in itself hardly sufficient to warrant the hypothesis of the existence in the secondary period of a continent (Lemuria) stretching between South Africa, Madagascar, and southern India, it is of interest to note that similar relationships in these several areas have been found also in other groups of animals (mammals, birds), and certain geologists have advocated this theory on the evidence of a similarity between the fossil plants and reptiles of South Africa and India. The theory was strenuously opposed by Wallace, who, on account of the great depths of ocean which separate the extensive shoals and coral reefs now to be found in the Indian Ocean between Madagascar and India, considered that there could not have been a continuous land surface during the secondary or tertiary periods, but admitted the former existence in those parts of several large islands, some of them not much inferior in size to Madagascar itself; and these islands he supposed were stepping-stones for an interchange of faunas. Nevertheless the Lemuria theory still has its champions, and, for instance, Major Alcock (A.M.N.H. 7.14.267) explains the distribution of the *Coeciliidae* and of some hermit crabs in terms of this same theory. Other writers, in order to explain a certain affinity between the land shells of Australia and those of southern Africa, have requisitioned the Antarctica theory, and Hedley indeed (A.M.N.H. 6.17.117) considers that there has been a direct or more probably indirect land connection through Antarctica between Australia and Africa; and Gilchrist ("Science in South Africa", p. 192), referring to certain genera of marine fish common to the Antarctic region and to South African waters, says that the "shore forms might be taken as additional evidence of the former existence of an Antarctic continent", but guardedly adds "an explanation postulating the existence or removal of continents is to be regarded as a last resource".

However this may be, it appears that the affinities of the South African lizards with those of other regions are to be paralleled, not only amongst other groups of animals, but also in the plants of the present day, for Bolus ("Science in South Africa") says that "the flora of the south-west Cape Colony presents striking marks of a similar origin to that of Australia", and Wallace states that "the affinities of the Madagascar flora are largely African, whilst Bentham emphasizes the fact that "the connection of the mascarene endemic compositae, especially those of Madagascar itself, are eminently with the southern and sub-tropical African races".

As regards the entity of the South African region as a zoological area, there can be no doubt but that the distinction between the peculiar endemic fauna of southern Africa and the fauna of tropical Africa is too pronounced to permit of our regarding the South African region as merely a province of the large Ethiopian area and indeed, but for the infiltration of tropical forms, no one would hesitate to unite South Africa with Madagascar as a region quite distinct from the more northern parts of Africa. But the question of the northern boundary of our area is quite another matter. It is obvious that under the circumstances the South African area must include all the southern African families and genera of Madagascar affinities, but as there are no strongly-marked natural boundaries, some few species, e.g. *Gerrhosaurus flavigularis*, have extended far into tropical Africa. I do not think it necessary to attempt to include the remotest limits of every widely-distributed species unless a sufficient number of species belonging to different genera extend thus widely but it must comprise the majority of the species. To fulfil these conditions the

South African zoological area should take in German East Africa (perhaps also British East Africa), British Central Africa, and Angola; that is to say, roughly speaking, Africa south of the equator, the Congo basin excepted. We should thus include the whole of the Zonuridae, practically all the Gerrhosauridae—though *G. flavigularis* apparently extends into Southern Egypt—and in addition to the genera previously mentioned in the Geckonidae, all the species of Pachydactylus, the genera Diplodactylus (Australia, Madagascar, and German East Africa) and Platypholis (German East Africa), an ally of Homopholis, in the Scincidae the allied genera Melanoseps and Sepsina which are related to Sepophis of Southern India, the genus Sepsina occurring also in Madagascar, and the genus Typhlacontias which is related to Acontias. The question may now be asked to what extent will the distribution of the other sections of the South African lizard fauna conform to the new arrangement. We have already seen that the families Agamidae, Lacertidae, Amphisbaenidae, and Varanidae form very few strongly-marked associations of species and still less of genera in the South African region as ordinarily defined, so that it could matter little if the distribution of these families should lend no support to this proposal for a greater South Africa. As a matter of fact, however, they are decidedly in agreement: in the case of a number of genera (Scapteira, Eremias, Nucras) certain representatives, either singly or in groups of species which occur in the western portion of the sub-continent, extend northwards into Angola and similarly genera in the eastern portion have species which are common to the Transvaal and German East Africa but not extending further north, or in these two areas are comprised all the species belonging to the same section of a large genus (cp. *Ichnotropis squamulosa*, the *hispida* section of *Agama*): and thus the proposed region would now include several additional genera peculiar to the area (Ichnotropis, Nucras) from which we may conclude that the comparatively recent Ethiopian fauna has really been in South Africa for a long period seeing that in this area peculiar genera have been evolved.

The present distribution of the Chamaeleons is somewhat puzzling, and, at first sight, difficult to explain in terms of the preceding hypotheses. According to Werner, the species constitute a number of structurally distinct groups, as follows:—The characteristic South African group goes along with a number of East African species and with the species common to the Seychelles and Zanzibar (Mocquard doubts the Zanzibar record for *C. tigris*; this is a point of considerable importance, in view of the great isolation of the Seychelles Islands): the distribution of the whole group almost coinciding with the larger South Africa. The species *anchietae*, of Angola, is considered by Mocquard (see Werner's monograph) to be identical with *lateralis* of Madagascar. This (or these) species belongs to a group which comprises another Madagascar species and two species from East Africa. The Indian, Arabian, Socotran, Syrian, North African, and Mediterranean species are all comprised in the section of nine species, which includes one West African species and three species occurring north of the equator stretching from west to east, two of them also extending far southwards (*dilepis* and *gracilis*). Another whole section of fourteen species is made up entirely of Madagascar and Comoro species. A section of ten species is composed of Madagascar and East African forms; and another section of nine species divides itself between the same two areas. Another section of ten species is made up of five West African (Kamerun and Gabun) species and five from East Africa. *C. namaquensis* is a section in itself.

The Chamaeleonidae have two other genera, *Brookesia*, confined to Madagascar, and *Rhampholeon*, of six species, which are distributed in East Africa from Mashonaland northwards to Somaliland. One species only extends from East Africa as far as Kamerun and Gabun in West Africa.

The salient facts shown by the above are : South Africa, East Africa, and Madagascar have mutual relationships, and these areas contain the great majority of the species. The most widely-distributed African species extend north of the equator stretching from east to west, and are comprised in the same section as includes the single Indian species, the widely-distributed *vulgaris* of North Africa and the Mediterranean region, the two Arabian species—one of which is also recorded from the Nile—and the Socotran species. These facts seem to me not inconsistent with the hypothesis which so well explains the distribution and affinities of the other lizards, and we may, indeed, suppose the Chamaeleons had their home in the large island which comprised southern Africa and Madagascar. After the separation of Madagascar and the union of northern and southern Africa certain species which have special facilities for distribution spread northwards, penetrating into Europe, and one odd species passed, via North Africa or Arabia, even into India and Ceylon.

The occurrence of Chamaeleons in all habitable parts of Africa and on numerous islands (Samo, Khio, Cyprus, Socotra, Comoro, Seychelles, Zanzibar, Mauritius, Bourbon, Canaries, and Fernando Po) undoubtedly points to the fact, which might not otherwise be suspected, that these creatures have exceptionally good capacity for distribution, and in this respect they differ widely from the other endemic groups of southern Africa (*Zonuridae*, etc.), which, as I think, have remained content with the area which formed their original home. Chamaeleon remains have been reported from Eocene deposits in Wyoming, U.S.A., and from Oligocene strata at Quercy, France, which, no doubt, indicates that Chamaeleons are a comparatively old group, and had an extensive distribution in past ages. We need not, therefore, suppose that Chamaeleons actually originated in the Ethiopian island, but only that all the present day Chamaeleons had their ancestors in that area.

According to Hollway ("Science in South Africa"), the northern boundary of South Africa, from a geographical point of view, is the great Congo-Zambesi divide, which stretches like a bridge from east to west across the continent from within a short distance of the Atlantic to the north end of Lake Nyassa; and I think it very probable that this boundary on the western half coincides with the northern boundary of the South African zoological area, but on the eastern side the highland area goes much further north, and so also does the South African fauna.

Mr. W. L. Sclater has proposed (*Geog. Journal*, 7, 282) to divide the Ethiopian region into four sub-regions, the Saharan, West African, Malagasy, and Cape sub-regions, and he then extended the Cape sub-region as far as the Congo watershed on the west and the Tana watershed on the east, which is entirely in agreement with my present conclusions; but, later on, he found it "increasingly difficult to draw any dividing line between the Saharan and Cape sub-regions" ("Science in South Africa", p. 150), and, limiting himself to the area south of the Zambesi and Cunene Rivers, he attempted to show that "South Africa has not such a specialized fauna as was formerly attributed to it, and that it has comparatively little to distinguish it from the rest of the Ethiopian region". Now this generalization was based on the question of percentages of peculiar genera

amongst the South African (south of the Zambesi and Cunene Rivers) land vertebrates; but a rigid statistical inquiry of this kind may often prove very misleading, for there are a number of genera (*Zonurus*, *Gerrhosaurus*, *Pachydactylus*) which have each many species the majority of which are confined to South Africa, but as one or two outlying species happen to have crossed the border the genus has no title to be called peculiar, and yet the evidence of such genera is clearly of considerable import; and, again, the genera which occur only in South Africa and in Madagascar are also misplaced in such a simple statistical scheme. But, as a matter of fact, this method would have led to a more correct conclusion had the author adhered to the Cape region as previously defined by himself.

It is not possible for me to say to what extent the distribution and affinities of the other South African land vertebrates is in accordance with the conclusions based only on the study of the lizards—but probably it will be found that every group of vertebrates resolves itself into two sections representing the ancient and the new faunas—and as for the invertebrates it is hardly to be expected that many groups distribute themselves according to vertebrate regions. However, Mr. Distant, from consideration of the Rhopalocera, is disposed to accept Selater's Cape region, but suggests that Somaliland should also be included (A.M.N.H. 7.1.47). Zoological regions have no absolute value and apply only to certain groups, seeing that the facilities for distribution vary immensely in the animal kingdom and that different groups of animals have arisen during different geological periods, and since their origin have been subjected to a great diversity of changes: and indeed a zoological area is chiefly interesting to the zoologist as a datum bearing on the history of the groups which conform to that area.

THE ZOOLOGICAL SUB-REGIONS OF SOUTH AFRICA.

The available data are still insufficient to deal at all thoroughly with this subject, but the broad facts of the matter are as follows: a western portion comprising Angola, German south-west Africa, west Cape Colony, and the Karroo, has a very characteristic fauna abounding in types which are structurally adapted for life in arid and sandy regions; an eastern portion, including German East Africa, Portuguese East Africa, British Central Africa, Rhodesia, low veld Transvaal, Zululand, Natal, and the eastern portion of Cape Colony, together with a part of the southern coastal strip, has also a distinct fauna. Between these two areas are included the Orange River Colony and the high and middle veld portion of the Transvaal, the fauna of which is more nearly allied to the western area though it is very much poorer in deserticolous types than is any portion of that western area. I believe, therefore, that in the southern portion of our sub-continent that extensive range of high mountains, the Drakensberg, marks the boundary between the eastern and western sub-regions, but it should be clearly understood this is not an absolute boundary for every species; northwards there is no natural boundary to separate the two areas but, nevertheless, Angola and German East Africa have faunas sufficiently distinct but no doubt with some overlapping.

The more characteristic fauna of the western region is as follows:—All the South African species of *Eremias*, and of *Scapteira*, the South African group of six species of *Mabuia*, including *trivittata*, *occidentalis*, etc., the geckonid genera *Ptenopus*, *Palmatogeco*, *Chondrodactylus*, *Rhoptropus*, and *Colopus*, the genus *Cordylosaurus*, and the species *Amphisbaena quadrifrons* *Monopeltis capensis*, *Typhlosaurus lineatus*, and *Chamaeleon*

namaquensis. As already stated, this fauna is concentrated in German South-West Africa, western Cape Colony, and the Karroo, whilst only comparatively few elements extend to the high central plateau constituted by the Orange River Colony and high and middle veld portions of the Transvaal; this central plateau, apart from the species which are undoubtedly representatives of the western fauna, has very few species peculiar to the area, and the rest of its fauna is made up of widely-distributed species, so that I do not think that this area is entitled to stand as a sub-region distinct from the western and of equal importance to it.

The headquarters of the typical western and eastern faunas are areas of widely different environment, the western portion being comparatively arid and rainless, whilst more genial conditions prevail in the eastern area. Consequently the western fauna shows to a considerable extent, structural adaptations with the surroundings, as for example in *Typhlosaurus lineatus* with its sharp cutting snout for burrowing in baked earth and burning sand; the species of *Scapteira* (Lacertidae) and the gecko *Ptenopus garrulus*, with their broadly-fringed digits, which allow of rapid movement over loose sand; *Chamaeleon namaquensis*, whose brown and sombre hues, assimilating with the desert colours, contrast strongly with the vivid greens of bush-frequenting chamaeleons.

The more characteristic fauna of the eastern region includes the following genera and species: In the Scincidae the species of *Herpetosaura* and *Melanoseps* and *Acontias plumbeus*; the geckonid genera *Homopholis*, *Platypholis*, and *Diplodactylus*; the degraded *Typhlosaurus aurantiacus* and *cregoi*; in the Amphisbaenidae three species, *Amphisbaena violacea*, *Monopeltis sphenorhynchus*, and the genus *Chirindia*; two species of *Agama*, namely, *kirki* and *mossambica*; the great majority of the species of *Rhampholeon* and probably *Chamaeleon damaranus* and *caffer*.

This eastern region extends along the southern coastal strip of Cape Colony for a considerable distance in a westerly direction, reaching as far as Knysna, though the most characteristic species of the region do not extend much further south than Zululand. In thus defining the southern limits of the eastern areas I have been guided to some extent also by the distribution of the widely distributed tropical species which extend southwards into our area. Such tropical species in all cases extend much further southwards on the eastern side than on the western side. In some cases, e.g. *Mabuia quinquecincta*, the species extends from Angola to East Africa, but southwards it scarcely penetrates into German South-West Africa, and avoids the high central plateau, but extends in a southerly direction into low veld Transvaal, Zululand, Natal, and Werner records it from the Grahamstown neighbourhood. *Lygosoma sundevalli* and *Ablepharus wahlbergi* have a similar distribution, but these species encroach somewhat further on the western side. *Mabuia striata*, the common house skink, occurs throughout the whole area with the exception of south-western Cape Colony. Much the same kind of distribution obtains amongst the tropical geckos. *Hemidactylus mabouia* appears to be altogether absent from German South-West Africa and the central plateau, but eastwards it extends into Barberton District and Zululand. *Lygodactylus capensis* again is absent from German South-West Africa, and from western Cape Colony, but occurs on the high plateau, extending as far south as Kimberley on the western side and Natal on the east side.

Chamaelon quilenis is found throughout the whole area with the exception of Cape Colony.

It will be seen from the above facts that the two areas are by no means homogeneous throughout their length, inasmuch as the tropical fauna from the north gradually loses in intensity as it passes southwards, whilst a somewhat opposite state of affairs obtains with the peculiar South African fauna. The rivers of South Africa, no doubt, act as efficient barriers against the dispersal of a small proportion of the species. On the west side, the Orange River seems to be the southern boundary of a number of tropical species which enter the western sub-region, and, consequently, in western Cape Colony the peculiar fauna of South Africa is relatively most strongly developed. On the east side the Limpopo River is apparently an impassable barrier to such typical South African lizards as *Mabuia trivittata*, *Pseudocordylus microlepidotus*, and *Chamaesaura aenea*; and, on the other hand, such tropical species as *Agama kirki* are not to be found south of that river.

It may be possible to further divide the western region, and, perhaps, also the eastern, into a number of zones according to altitude, but there is not sufficient data to determine this. It is known, however, that there are certain species (*Zonurus cordylus* and *Mabuia homalocephala*) which occur only on the coastal strip of South Africa.

In conclusion, we may summarize as follows:—The South African zoological region is sub-divided into western and eastern sub-regions with the limits as above defined, but the separation is not a very profound one, for some species and many genera are common to both sub-regions, and, though some genera and many species are absolutely confined to one of the regions only, this cannot be said of any natural group of genera nor of any family of lizards, whilst, lastly, the segregation is largely in accordance with different environmental conditions, seeing that the most characteristic elements of the western sub-region show many structural adaptations for a deserticolous habitat.